FIRST RECORD OF AN HETEROTIC, ADULT FEMALE HYBRID *LIMENITIS (BASILARCHIA)* RUBIDUS (LEPIDOPTERA: NYMPHALIDAE)[1]

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ABSTRACT: The interspecific hybrid cross *Limenitis arthemis astyanax* x *L. archippus* yields the intermediate hybrid morph *L.*"rubidus" (Strecker). Such F_1 hybrids occur in nature but they are quite rare; those reported to date have all been males. Laboratory crosses generally are lethal to females (which are heterogametic), with most dying during development; only a few have eclosed as malformed adults. This paper reports a laboratory cross that produced the first known heterotic female specimen of this remarkable F_1 morph. It is intermediate between two related species of mimetic butterflies which are completely unlike in phenotype.

Interspecific hybridization among the four widely distributed species of Nearctic admiral butterflies *Limenitis (Basilarchia)* has been well-documented (Field, 1904; 1914; Nakahara, 1924; Hovanitz, 1949; Remington, 1958; 1968; Platt, 1975; 1983; 1987; Platt *et al.,* 1978; Ritland, 1990; Kemp, 1991; Platt & Maudsley, in revision). Except for crosses involving the two subspecific forms *L. arthemis arthemis* (Drury), and *L. arthemis astyanax* (Fabr.) (which in this report, as in the earlier papers by Platt and his co-workers, are considered to represent a single polymorphic species), these insects rarely hybridize in the wild (see White, 1990).

Such hybridization occurs among other closely related species within different insect groups as well, *e.g.* Saturniidae (Tuskes & Collins, 1981), Gerridae (Wilcox & Spence, 1986), and Libellulidae (Tennessen, 1981). The viability of such crosses, however, is variable. Bick & Bick (1981) report 93 hybrid pairings among Odonata involving ten families, 24 genera, and 124 species. Only two of these (one of which is questionable, due to the probability of sperm precedence) resulted in hybrid offspring.

In *Limenitis*, the cross involving *L. archippus* (Cr.) and *L. arthemis astyanax* is heterogametically inviable (Platt, 1987), usually producing

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no normal F_1 adult females. The males develop normally and are fertile in backcrosses to parental stock females (Platt, 1975; 1983). All 43 of the known wild-collected hybrid specimens are males. In laboratory crosses using Platt's (1969) hand-pairing method, 43 females (6.4%) among 628 adults occurred (Table 1). All other females died as eggs, larvae, or prepupae (determined to be female by Kean & Platt's, 1973 methods), or else formed hibernacula as third instar larvae, even though they were in long-day photoperiod (16L:8D). Normal *Limenitis* larvae (hybrid and non-hybrid) do not exhibit diapause responses when reared in > 11 hr light (Platt & Harrison, 1988). The few females that did eclose all metamorphosed early, at the end of the fourth larval instar. These, without exception, were stunted, malformed, faded in wing color, unable to fly, and infertile (Fig. 2). The broods in which females occurred generally involved parental strains from geographically distant areas such as northern Vermont and central Maryland (see Platt, 1987; Platt *et al.*, 1978). The stunted females make up only 1.3% of the progeny from crosses involving *L. archippus* and *L. arthemis astyanax* collected in the same geographic area (Table 1). These crosses have been made reciprocally between the sexes of the two species.

Table 1 also shows 441 males and four females were reared among 19 broods involving crosses of the two species obtained from the same regions (type A). Ten broods arising from hybrid crosses made between strains from different localities (type B) produced 187 males and 39 females. A 2 x 2 contingency test for the overall male and female values for stocks originating from A) the same, or B) different geographic regions yields $\Sigma X_1^2 = 66.82^{**}$, with $P < 0.01$. This highly significant result demonstrates that more adult females develop when stocks of the two species originating from different geographic regions are crossed. However, as the table makes clear, this difference arises from the nearly complete fertility of two hybrid crosses reared in 1973, in which a single male *L. archippus* from Vermont was hybridized to two sibling female *L. arthemis astyanax* from Maryland.

Thirty wild-collected specimens involving crosses between the broadly sympatric *L. archippus* and its congeneric species *L. arthemis arthemis* (n=11), *L. weidemeyerii* Edw. (n=10), and *L. lorquini* Boisd. (n=9) have been recorded by Platt & Maudsley (in revision). (The above allopatric butterflies are more closely related to each other than they are to *L. archippus*—see Platt, 1983). These F_1 hybrids also are all males and exhibit variable intermediate phenotypes.

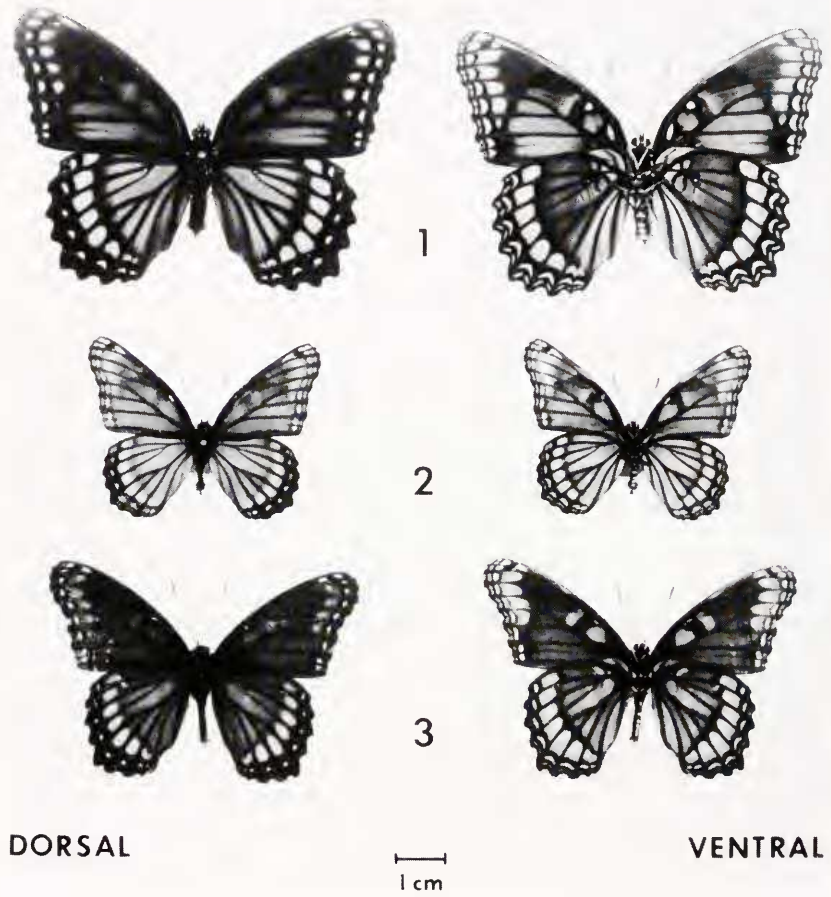
A recently reared brood (*L. archippus* ♀ x *L. a. astyanax* ♂), however, included one heterotic F_1 female, plus 97 males. The lone female

eclosed 14 days after her siblings. Both P_1's were of Maryland stock. The fertility of this specimen is unknown, as the age and condition of the remaining males made attempting to breed her impossible. Fig. 1 shows the F_1 heterotic *L.* "rubidus" female; a typical stunted female hybrid is shown in Fig 2, and a typical wild-collected hybrid male in Fig. 3. All laboratory bred *L.* "rubidus" males have been similar in size and coloration to this wild-collected specimen, although they vary somewhat in the amount of dorsally expressed orange.

Heterotic F_1 females similar to the one in Fig. 1 occur when the three allopatric species of Nearctic *Limenitis* (*L. arthemis, L. lorquini, and L. weidemeyerii*) are crossed. Such individuals are larger, and more robust than those of the pure-bred species. These hybrid females so far have proven to be infertile when crossed to male siblings except in two cases, one involving a New England *L. a. arthemis* ♀ x an *L. lorquini* ♂ from Oregon, and the other involving an *L.a. astyanax* ♀ from Maryland x an *L. weidemeyerii* ♂ from Colorado. In the first cross-type the F_2's are phenotypically variable, but many closely resemble *L. lorquini*; in the second cross-type the progeny all are hybrid-like in appearance. Dissections of these heterotic females reveal that many of them possess undeveloped reproductive structures and lack eggs. Similar hybrid-like females result from backcross broods involving the hybrid *L.* "rubidus" males (Platt, 1983; Platt *et al.*, 1978). These females often prove to be infertile when bred to parental stock males. Several such backcrosses, however, have been reared over the years and resulted in large broods.

Interspecific crosses among Lepidoptera, including those involving *Limenitis*, are variable in terms of their viability. Most of our laboratory matings are infertile. However, occasional broods exhibit nearly complete egg hatching, and many male progeny. Such was the case with the brood which produced this unique robust F_1 female, resulting from the union of genetically compatible gametes representing two closely related, but distinct species. Admiral butterflies for the most part conform to Haldane's (1922) Rule among interspecific hybrids, but the survival of this heterotic individual is a clear exception to it. Apparently this female, unlike previously known hybrid specimens, had a compatible genetic makeup allowing for full morphological development. Why her development was so delayed relative to that of her male siblings must have been dependant on the titres of ecdysone and juvenile hormone present in this particularly large individual.

Our results demonstrate the close affinities existing between the *L. archippus* and *L. arthemis-astyanax* species groups of eastern North America. Gene exchange and gene flow between the two complexes takes place only rarely in the natural environment, but it provides a



Figs. 1-3—Laboratory-bred and wild-collected specimens of interspecific hybrid form L."rubidus" Strecker (*L. a. astyanax* x *L. archippus*): 1) unique heterotic F_1 female reared from first generation Maryland strains; raised on weeping willow, (*Salix babylonica* L.). 2) typical weakened and stunted F_1 female, as rarely obtained in such crosses (see text). This specimen was reared on wild or black cherry (*Prunus serotina* Ehrh.). 3) Typical wild-collected male specimen from near Dover (Kent Co.), Delaware, taken in late Sept. 1943. From an old, local natural history collection, Accession No. 1341, Leg. L. Darr of Middletown, Md. Laboratory-reared males are similar in size and appearance to this latter specimen. All specimens are now in the UMBC collection.

means by which alleles may be passed from the one complex to the other. Indeed, if the rare F_1 hybrids can backcross in nature such introgression could lead to rapid evolutionary modifications which, perhaps, have played an important role in the evolution of the mimetic color patterns of the adult insects.

Table 1—Comparison of hybrid *L.* "rubidus" ♂ vs. ♀ progeny from parental stocks of the two species originating from A) the same, or B) different geographic locations.

Location		No. of Broods	No. of ♂♂	No. of ♀♀	%♀♀
A) Mid-Atlantic[1] x Mid-Atlantic or New England[2] x New England:					
P_1 ♀♀	P_1 ♂♂				
1) *L. archippus*	*L. a. astyanax*[3]	4	80	0	0
L. a. astyanax	*L. archippus*[3]	5	52	0	0
Subtotal:		9	132	0	0
2) *L. archippus*	*L. a. astyanax*[4]	5	204	1*	0.5
L. a. astyanax	*L. archippus*[4]	5	105	3	2.8
Subtotal:		10	309	4	1.3
B) New England x Mid-Atlantic:					
3) *L. a. astyanax*	*L. archippus*[5]	5	104	39†	27.3
4) *L. a. astyanax*	*L. archippus*[6]	4	62	0	0
5) *L. archippus*	*L. a. astyanax*[6]	1	21	0	0
Subtotal:		10	187	39	20.9
Total:		29	628	43	6.4

[1] Mid-Atlantic includes strains from Delaware, Maryland, and New Jersey.

[2] New England includes strains from Connecticut, Massachusetts, and Vermont.

[3] Platt (1975), [4] Platt (1987), [5] Platt *et al.* (1978), [6] Platt (Unpubl. data).

* This is the heterotic ♀ that is the subject of this paper.† Thirty-three of these represent 2 broods with the same P_1 ♂ and sibling P_1 ♀♀. Sex ratios of both broods were ~1: 1 .

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